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# Temporal and spatial variability of zooplankton on the Faroe shelf in spring 1997–2016



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## ABSTRACT

Zooplankton availability during spring and summer determines the growth and survival of first-feeding fish larvae, and thus impacts the recruitment to both fish prey species and commercial fish stocks. On the Faroe shelf, however, the relative importance of oceanic versus neritic zooplankton species has hitherto not been well understood. In this study, spatio-temporal variability in zooplankton community structure and size spectra on the Faroe shelf is investigated using observations from late April during the period 1997–2016. The main objective was to explore which environmental variables influence the zooplankton community structure in early spring. The zooplankton community in the permanently well mixed central shelf inside the tidal front consists of a mixture of neritic, cosmopolitan and oceanic species. In this region, redundancy analyses showed that chlorophyll concentration had a positive effect on abundance of neritic copepods and meroplankton as well as all zooplankton < 1.2 mm. The abundance variability of these species shows increased production around 2000 and 2008–2009. The highest zooplankton abundance, mainly consisting of *Calanus finmarchicus*, is however observed off-shore from the tidal front, especially on the western side of the Faroe Plateau. A shift in *C. finmarchicus* phenology occurred around 2007, resulting in earlier reproduction of this species, and this variability could not be explained by the employed regional environmental parameters. Our results indicate that the Faroe shelf biological production is more dependent on the local primary production and neritic zooplankton species than on the large oceanic *C. finmarchicus* stock.

## 1. Introduction

The Faroe shelf sustains several economically important fish stocks including cod, haddock and saithe (ICES, 2016), which spawn during spring (Steingrund et al., 2005). Earlier studies have revealed a close relationship between primary production and fish recruitment and fish growth (e.g. Eliassen et al., 2011; Gaard et al., 2002; Steingrund and Gaard, 2005). Zooplankton is a critical trophic link between phytoplankton and fish prey species, commercial fish stocks and seabirds, although details in such links are still poorly understood (Eliassen et al., 2011). In this context it is important to better understand the variations in zooplankton abundance and their associations with physical changes in the marine environment. The Faroe Marine Research Institute's monitoring programme on biological oceanography around the Faroe Islands started in the 1990s with sampling stations covering the central part of the shelf and to a lesser extent also the outer shelf waters. The present study is based on material sampled during the last week of April. This recurrent cruise has been placed at a critical time in spring

(late pre-bloom and early bloom phase) enabling investigations on the match-mismatch between the spring bloom development, subsequent zooplankton reproduction and community development and occurrence of first-feeding fish larvae.

In previous studies, the Faroe Plateau has been divided into exclusive domains based on oceanography (e.g. Larsen et al., 2009, 2008) and recently also on phytoplankton variability (Eliassen et al., 2017). One main division is formed by the tidal front at the approximately 100–150 m bottom depth contour, which separates the permanently well mixed central shelf (hereafter CS) from the surrounding seasonally stratified outer shelf (Fig. 1) (Hansen et al., 2005; Larsen et al., 2009, 2008). Off the Faroe Plateau, the water in the upper layers (0–500 m) is dominated by warm and saline pole ward flowing Atlantic water. In the near-bottom layer, cold and less saline overflow water flows equatorwards from the depths of the Norwegian Sea through the Faroe-Shetland Channel and the Faroe Bank Channel into the North Atlantic Ocean (Hansen and Østerhus, 2000). The temperature and salinity on the Faroe Plateau is generally higher on the western side, and lower on the

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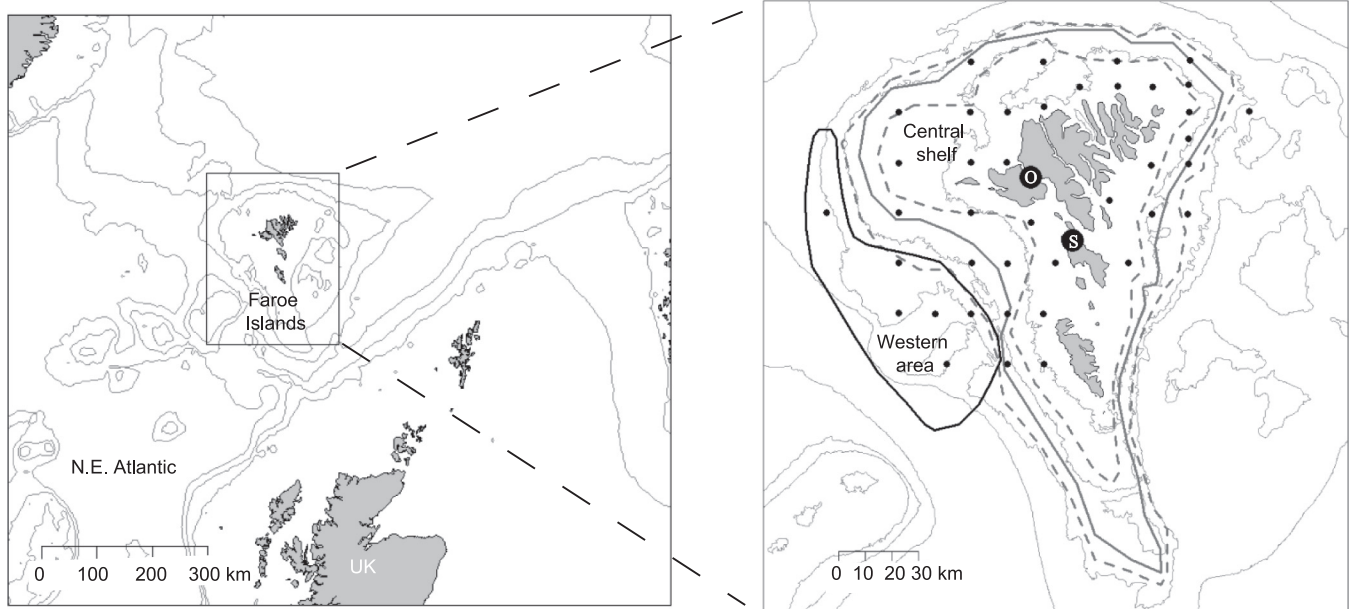


Fig. 1. Map of the North East Atlantic (left) and the Faroe shelf (right). The thick grey lines on the map of the Faroe Shelf shows the average position of the front and the area between the grey dashed lines cover a depth interval equal to two standard deviations from the average front position (from Larsen et al., 2009). The well mixed area inside the shelf front is denoted central shelf (CS). The black dots represent stations typically sampled on the standard cruise in late April. ‘O’ and ‘S’ denote fixed coastal stations on the shelf, while the area inside the thick black line shows position of the outer western area (W) (see Section 2.3 for definition of areas). The grey lines represent 200, 500 and 1000 m bottom depth contours and 100, 150, 200 and 500 m bottom depth contours in the left and right panel, respectively.

eastern side. This is due to the influence of the relatively warm and saline North Atlantic Current coming from the south-west. As this water crosses the Iceland-Faroe Ridge in a clock-wise path around the Faroe Plateau, it is cooled and freshened due to a combination of atmospheric influence and admixture of colder and less saline water north of the ridge (Larsen et al., 2012). Due to effective winter cooling in the shallow waters and excess precipitation over land, the temperature and salinity during spring in the CS are respectively  $\sim 1^\circ\text{C}$  and  $\sim 0.1$  psu lower than in the outer shelf waters (Larsen et al., 2009). The average residence time of the CS water is estimated to be 1–2 months, but is likely highly variable (Eliassen et al., 2016; Larsen et al., 2008; Rasmussen et al., 2014). The separation of the CS from the outer shelf supports separate planktonic species and interannual variation in phytoplankton abundances on the shelf have led to an exchange-hypothesis, which suggests that variable cross-shelf exchange dilutes the phytoplankton biomass inside the tidal front, and thus induces variations in the phytoplankton accumulation (Hansen et al., 2005; Eliassen et al., 2005; Eliassen et al., 2016). This mechanism seems to explain some of the variability in phytoplankton biomass prior to June (Eliassen et al., 2016). The zooplankton community within the CS basically consists of neritic species, although it is also influenced by variable amounts of oceanic species (Gaard, 2003, 1999). Oceanographically, as well as biologically, the waters in the CS and the outer shelf are therefore quite different. The CS ecosystem is relatively spatially confined making it well suited for ecological studies.

On the Faroe shelf the phytoplankton spring bloom usually occurs in April–May, but it is highly variable, both in timing and in magnitude (Debes et al., 2008b; Hansen et al., 2005). Inside the  $\sim 120$  m bottom depth contour, the zooplankton species composition in spring is a mixture of neritic copepod species (mainly *Temora longicornis* and *Acartia* sp.), meroplankton (e.g. cirripedia larvae, decapod larvae and polychaete larvae), cosmopolitan zooplankton species (e.g. *Pseudocalanus* sp., appendicularians and chaetognaths) and oceanic zooplankton species, which are advected from the offshore environment (Gaard, 1999). The biomass in the zooplankton community during spring and early summer is usually dominated by the large, oceanic copepod *Calanus finmarchicus* (Debes et al., 2005; Gaard, 1999). The deep overflow

transports large quantities of overwintering *C. finmarchicus* from the deep Norwegian Sea (Gaard, 1999) through the Faroe Bank Channel west of the Faroes (Heath and Jónasdóttir, 1999). The northern Irminger Sea and Iceland Basin are also centres of overwintering *C. finmarchicus* (Heath et al., 2000) from where individuals can be carried toward the Faroes with the north eastward directed Atlantic inflow branch (Hansen and Østerhus, 2000). Between late March and late April the overwintered individuals migrate toward the surface (Gaard and Hansen, 2000). Import of *C. finmarchicus* onto the Faroe shelf during spring after the individuals have ascended to the upper layer requires horizontal advection and thus, this transport will vary according to the exchange rate. Investigations on the zooplankton abundance in the CS have shown interannual variations, where the ecosystem shifts between dominance of neritic zooplankton species some years (e.g. 1993–1995 and 2000) and horizontally advected oceanic species other years (e.g. 1996–1997) (Gaard, 2003, 1999).

In recent years recruitment to the Faroe cod and haddock stocks has failed (ICES, 2016). This failure is partly a result of high fishing mortality, but natural environmental variability also appears to be important (Steingrund and Gaard, 2005). The role of zooplankton in these changes is stimulating this particular study as survival of first feeding fish larvae during the early life phase is a well known bottleneck in fish recruitment (Hjort, 1914). The larvae feed on zooplankton and phenological synchronization between the larvae and zooplankton is a prerequisite for larval survival (Cushing, 1990). The available studies of the zooplankton community on the Faroe shelf in spring are one-two decades old (Debes and Eliassen, 2006; Gaard, 2003, 1999). They document large variations in the abundance and community structure of the zooplankton, but the data on zooplankton only includes taxonomic abundances, not sizes. With regards to feeding conditions of fish larvae, taxonomic abundances are important, but equally or perhaps more important is the size spectra of the zooplankton (Frank and Leggett, 1986). Because the zooplankton assemblage in the CS is composed of zooplankton from different geographical origins and with different life strategies (Debes and Eliassen, 2006; Gaard, 1999), the species may respond differently to changes in regional temperature and food concentration, and their abundance may also change as a result of

**Table 1**  
Grouping of zooplankton taxa based on species traits along with their overall relative (%) contribution to the group in numbers. Note: G<sub>0</sub> refers to the parental generation, while G<sub>1</sub> refers to first generation individuals.

Group	Taxa	Contribution (%)
Copepod eggs	All species	
Copepod nauplii	All species	
<i>C. finmarchicus</i> CI-CIII (i.e. G <sub>1</sub> = recruits)	<i>C. finmarchicus</i> CI-CIII	
<i>C. finmarchicus</i> CIV-CVI (i.e. G <sub>0</sub> = overwintered individuals)	<i>C. finmarchicus</i> CIV-CVI	
Other	Appendicularia	10
	Chaetognatha	1
	Harpacticoida	45
	Krill eggs	2
	Krill nauplii	5
	<i>Oithona</i> sp.	22
	<i>Pseudocalanus</i> sp.	7
	Pteropods	8
Neritic copepods	<i>Acartia</i> sp.	67
	Large <i>T. longicornis</i>	33
Meroplankton	Cirripedia cyprids	4
	Cirripedia nauplii	48
	Decapod larvae	6
	Fish eggs	1
	Polychaete larvae	5
	Unidentified eggs	36

mixing processes e.g. horizontal advection as well as the concentrations of zooplankton in surrounding oceanic waters. The present study gives the first presentation of a comprehensive spatio-temporal dataset of the zooplankton community and size structure in the Faroe shelf area from annual cruises in late April 1997–2016, and links the observed population dynamics to relevant explanatory variables.

## 2. Materials and methods

### 2.1. Data collection

The data and sample sets were collected with R/V Magnus Heinason on annual standard cruises during the last week of April on the Faroe Plateau during the period 1997–2016 (except for 2002 when the cruise was cancelled). Stations typically occupied on the cruise are shown in Fig. 1, but the number of stations varies from year to year due to inclement weather some years. Sampling was carried out between 6:30 and 18:30 and thus should not be markedly affected by diel vertical migration.

#### 2.1.1. Hydrography

Temperature and salinity were measured with a Seabird Electronics SBE911plus CTD (Conductivity, Temperature, Depth), equipped with a rosette sampler. In situ fluorescence was measured with a fluorometer, interfaced to the CTD. Fluorescence was calibrated from selected samples, which were analysed spectrophotometrically for chlorophyll *a* (chl) (Parsons et al., 1984). Salinity samples (for calibration of the CTD) were measured using an Autosol salinometer.

#### 2.1.2. Zooplankton

Zooplankton samples were collected with a Bongo net (diameter 0.6 m) with a mesh size of 100 µm. The net was lowered slowly down to 50 m depth and up again, while the ship was towing at a forward speed of about 2.5 knots. Thus, the samples were collected in a V-shape in the upper 50 m. No regards were taken of possible upper layer stratification. The volume of the filtered water was measured with a Hydro-Bios flowmeter mounted on the nets openings. The samples were preserved in 4% formaldehyde.

In the laboratory, preserved zooplankton samples were purged of

formaldehyde and sub sampled with a Motoda cylinder splitter. Processing of the aliquots was done by automated analysis using the Epson Perfection V700 Photo Scanner for image acquisition and the Zoolmage software for analysing the images obtained. See Bachiller and Fernandes (2011) and Grosjean and Denis (2007) for details on the sample handling and image processing of the Zoolmage software. This approach was chosen as it takes significantly less time than the traditional methodology (Bell and Hopcroft, 2008; Gislason and Silva, 2009).

Two training sets were built for the study area in order to identify the zooplankton groups. The samples were sorted according to bottom depths < 150 m (shallow) and ≥ 150 m (deep), respectively. The 150 m bottom depth contour is generally the outer boundary of the shelf front (Larsen et al., 2009) which separates the oceanic ecosystem from the shelf ecosystem (Gaard, 1999), and building two training sets was necessary in order to maximise the recognition accuracy of zooplankton in the oceanic ecosystem. A total of 18 classes (artefacts excluded) were found to properly represent the zooplankton community in the shallow training set based on their occurrence and abundance. In comparison, the training set representing the deep water samples only included 11 classes as meroplanktonic species and neritic copepod species were basically absent. The taxonomic classification was carried out using the Random Forest algorithm (Breiman, 2001) as it scored the highest in accuracy. The performance of the classifier was assessed by calculating a 10-fold cross-validation matrix between the manual and the automated classifications. The recognition accuracy was obtained to 94.8% and 91.1% for the deep and shallow classifier, respectively. Eggs and large copepods had the lowest cross validation error estimation (< 10%), while copepod nauplii and small to medium-sized copepods had higher error estimation (10–20%). Small *T. longicornis* had very high error estimation (43%) and they were therefore excluded from further analyses regarding zooplankton taxa groups. The low recognition accuracy of small zooplankton is likely a result of the low resolution of the scanned images. Data for abundance of zooplankton taxa and sizes (measured as equivalent circular diameter, ECD) were obtained for each object identified in the digitised images. After the initial classification zooplankton taxa were merged into species groups (Table 1) based on ecological knowledge of the taxa (from Gaard, 1999) supported by an Agglomerative Hierarchical Clustering (AHC) (Lance and Williams, 1967) analysis performed on taxa abundances in all samples (Fig. S1). Cosmopolitan holoplanktonic species (i.e. *Oithona* sp., *Pseudocalanus* sp., Harpacticoida, Appendicularia and Pteropods) and species with low abundances (i.e. Chaetognatha, Krill eggs and Krill nauplii) were grouped as 'Other'. Size estimates were furthermore sorted into 0.4 mm size intervals and the abundance of each size group for each sample was calculated.

### 2.2. Additional data

In addition, average temperature, salinity and chl from April 20th–April 30th from coastal stations (Fig. 1) are presented together with the cruise CTD data. Temperature was measured at coastal station O using Aanderaa, Sensordata and recently Starmon temperature recorders, while salinity samples were collected at station S and measured using an Autosol salinometer (Larsen et al., 2008). At station S samples were also collected for chl measurements, which were analysed spectrophotometrically (Parsons et al., 1984).

Gridded near-surface satellite chl data from the GlobColour Project, distributed by ACRI-ST (<http://www.globcolour.info>), were used as phytoplankton indicator for the Faroe shelf area. Eight-days temporal average, level 3, merged (SeaWiFS, MODIS, MERIS, VIIRS in varying constellations), GSM-gridded (Maritorena et al., 2002) chl (CHL1) with 4-km grid resolution was downloaded for the period 1998–2016. Bloom initiation was identified as the first day of the year when the chl concentration reached ≥ 0.65 mg m<sup>-3</sup>. Bloom initiation from coastal station S was identified as the first day of the year when the chl

concentration reached  $\geq 1.05 \text{ mg m}^{-3}$ , as the in-situ values are generally higher than the remote sensing values (Eliassen et al., 2017).

In the Faroe Plateau area temperature largely controls water density (Larsen et al., 2009). Therefore, using atmospheric heat flux and temperature difference between the CS and the outer shelf waters, the average flux of energy through the tidal front in winter was estimated and subsequently converted into an average horizontal exchange rate,  $k$ , for the period 1992–2013 in Eliassen et al. (2016). This time series has been updated according to the method described in Eliassen et al. (2016) for 2014–2015. The estimated exchange rate, which can be interpreted as a volume flux through the front, contains no spatial or seasonal variation, but is an average representing the whole shelf during the months January–April.

### 2.3. Data processing and analyses

In total, data from 897 CTD stations and 359 zooplankton stations were analysed. However, the zooplankton observations are spatio-temporally highly scattered (Fig. S2). The data from each of the annual surveys were therefore first gridded onto a regular ( $0.25^\circ$  latitude  $\times$   $0.5^\circ$  longitude) grid using Objective mapping (Böhme and Send, 2005). Regions with sparse sampling, where the associated error map exceeded a selected threshold, were trimmed off, and the resulting spatial coverage is shown in Fig. S3. Gridded pixels with valid data points in at least three years out of the time series (1997–2016) are included in the temporal averages. In order to emphasise the spatial zooplankton distribution, the annual maps have been normalised by the spatial average over the survey domain. The data are presented as averages over the observation period, while the individual surveys are provided in the Supplementary Material (Fig. S2).

The sampling area was divided into two distinct oceanographic zones following previous analyses (Eliassen et al., 2017; Larsen et al., 2009) and the present spatial analysis of the zooplankton data (Fig. 5):

- i. central shelf (CS): The position of the shelf front is not stationary (Fig. 1). Thus, CS stations were here identified as stations inside the 130 m bottom depth contour where the temperature difference from 0 to 50 m was  $< 0.2^\circ\text{C}$  as this is presumed to be an indicator of the characteristic well mixed CS water (Larsen et al., 2009).
- ii. western area (W): An area on the outskirts of the western side of the outer shelf was carefully constructed based on the oceanographic and biological characteristics of the area and frequency of sampled stations (see Fig. S2).

Bottom depth characteristics for the two areas are summarised in Table 2.

For each station calibrated temperature and salinity values were averaged over 0–50 m depth while chl was averaged over 6–50 m (as the uppermost 5 m are usually affected by large signal-to-noise ratio), so as to be comparable to the zooplankton results. CTD temperature profiles from the two areas are shown in Fig. S4. The profiles verify the homogeneity of the CS water, while profiles in the W area were more heterogeneous showing occasional upper layer stratification. Sensitivity analysis were performed on temperature and chl depth profiles. A comparison between 0–20 m and 0–50 m averages in the two areas showed very similar results (Fig. S5), and effects of possible upper layer stratification were therefore ignored.

As the number and location of the sampling stations varied between

**Table 2**  
Bottom depth (m) characteristics for the CS and W area, respectively.

Area	Average depth	Min.	Max.
CS	85	56	116
W	257	153	813

years, the annual values (Figs. 3 and 4 and Figs. 6 and 7) are presented as spatial averages over the two areas. Redundancy Analyses (RDAs) were used to detect causality between environmental explanatory variables and abundance of zooplankton groups. RDA is the direct extension of multiple regression to the modelling of multivariate response data (Legendre and Legendre, 1998). RDAs were run on yearly averages. Year was set as conditioning variable in order to remove any effects that time may have had on the zooplankton abundances. Both response and explanatory variables were centred and reduced before the analysis. The statistical significance of correlations extracted from the RDAs was estimated by Monte Carlo permutation tests (999 simulations). Significance level was set at 0.05. Statistical analyses were performed in XLstat and R.

## 3. Results

### 3.1. Validation of ZooImage

ZooImage has been validated in a number of articles (e.g. Bell and Hopcroft, 2008; Di Mauro et al., 2011; Gislason and Silva, 2009; Irigoien et al., 2008; Lindgren et al., 2013; Vu et al., 2014), but the ability of ZooImage to correctly identify particles is directly related to how well the training set represents and encompasses the zooplankton present in the samples to be analysed (Culverhouse et al., 1994; Embleton et al., 2003). Therefore, to access the performance of the ZooImage software, 22 randomly selected samples covering the whole study area were also processed manually by traditional taxonomic procedure and compared with that of ZooImage (Fig. 2). Prior to the analysis, abundances were log-transformed to satisfy tests for heteroscedasticity and normality. An inspection of the coefficients of determination of the linear regression equations confirms the generally good agreement between the two methodologies. However, in all groups, except for *C. finmarchicus* copepodite stages CI–CIII, ZooImage had a tendency to overestimate the abundances (Fig. 2). This was probably mainly due to the low image resolution and the large amount of non-zooplankton particles (e.g. marine snow, litter, detritus, air bubbles, phytoplankton) in the samples leading to misidentification between non-zooplankton particles and actual zooplankton.

### 3.2. Hydrography

Upper layer (0–50 m) temperature and salinity variations for the Faroe shelf area in late April are shown in Fig. 3. In the CS, temperatures fluctuated between  $6.1^\circ\text{C}$  and  $7.9^\circ\text{C}$ . Average CTD values corresponded well with measurements from the coastal stations (Fig. 3). In the W area temperatures were higher, between  $7.3^\circ\text{C}$  and  $9.1^\circ\text{C}$  (Fig. 3a). The salinity variations resembled the temperature variations with few exceptions (Fig. 3b).

### 3.3. Phytoplankton

In general, the phytoplankton biomass both in the CS and W area during late April reflect a pre-bloom situation with low chl values (average  $\sim 0.5 \text{ mg m}^{-3}$ ) (Fig. 4a). Chl was on average highest in the CS with an inclination to the western side (Fig. 5h). Year 2000 stands out as a year with very high chl in the CS (Fig. 4a). The chl concentrations derived from the satellite were  $\geq 0.65 \text{ mg m}^{-3}$  at the time of sampling in year 2000 and (2008–2009) 2010 in the CS indicating that the onset of the spring bloom had already occurred, whereas in the remaining years the onset of the bloom had not occurred during the time of sampling (Fig. 4b). In the W area bloom initiation was always post sampling (Fig. 4b). The difference in average chl and bloom initiation between the two areas was not statistically significant ( $p = 0.054$  and  $p = 0.056$ , respectively (two-samples *t*-test)).

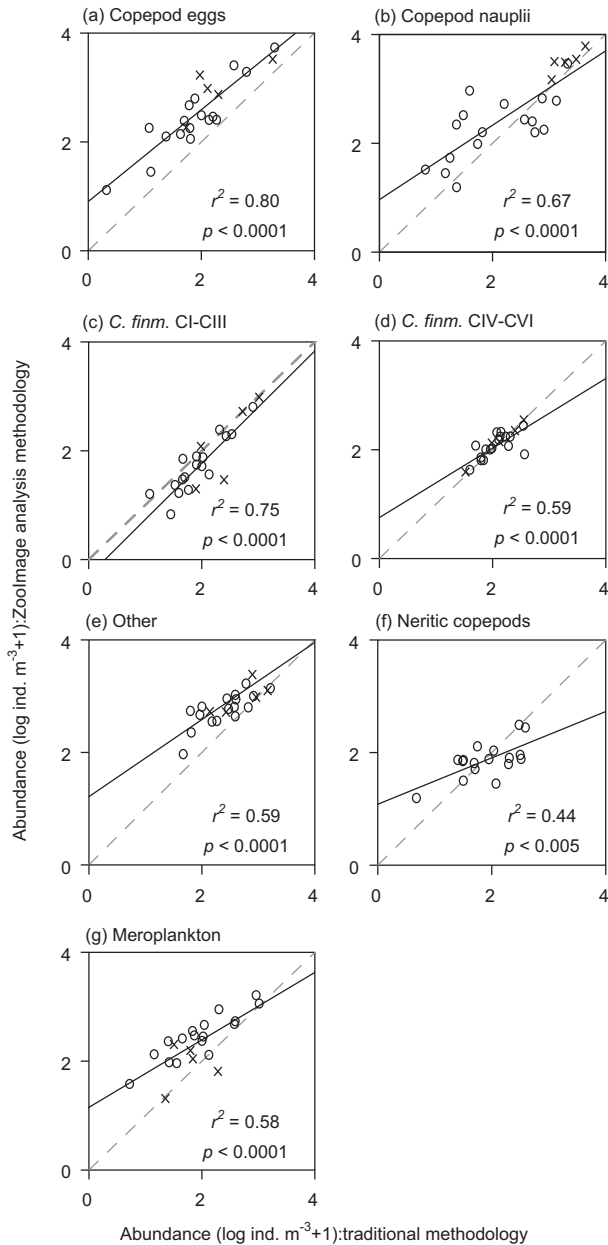


Fig. 2. Scatter plots of log-transformed abundance estimates based on manual classifications and automated ones using ZooImage. Open circles indicate samples taken at bottom depths < 150 m, while crosses indicate samples taken at bottom depths > 150 m. The continuous straight line represents best fits of the linear regressions, while the dashed line is the 1:1 line. Proportion of variance explained ( $r^2$ ) are given together with their respective significance values ( $p$ -value).

### 3.4. Zooplankton horizontal distribution

The spatial segregation into CS and outer shelf/oceanic zooplankton species is evident in the gridded climatological maps (Fig. 5a–g). Copepod eggs showed two main abundance regions: one covering the W area, shortly outside the shelf front i.e. the area with highest abundance of overwintered *C. finmarchicus* and one in the northern CS area (Fig. 5a). It is likely that the eggs in the W area mainly belong to *C. finmarchicus* while the eggs in the CS belong to a mixture of various (most likely neritic) species. The abundance of Copepod nauplii, *C. finmarchicus* and Other was greatest in the W area (Fig. 5b–e), indicating that this may be the main influx area of these assemblages in early spring. The groups Neritic copepods and Meroplankton (i.e. larval stages of various benthic fauna) are limited to the CS, in-shore of the tidal front (Fig. 5f–g).

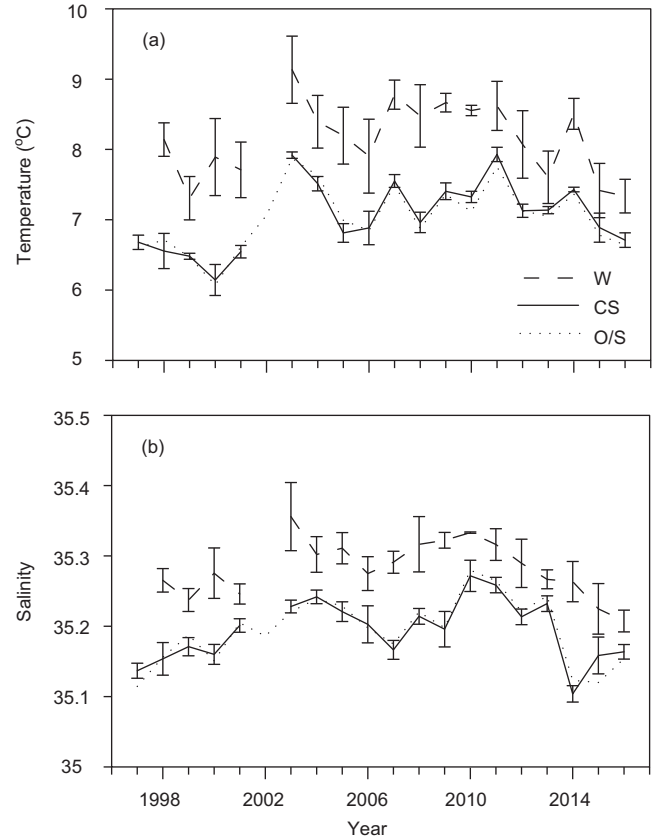


Fig. 3. Average (0–50 m) temperature (a) and salinity (b) from CTD stations in late April 1997–2016 in the CS and W area and contemporary values from coastal station O and S, respectively. Vertical lines show spatial standard deviation. Standard deviation was not computed for the time series from stations O and S.

### 3.5. Zooplankton interannual variability

Both in the CS and W area, the average abundances of zooplankton fluctuated greatly between years (Fig. 6). However, the abundances in the CS and W did not co-fluctuate. In the CS the highest values were observed in 2000 and 2013 (Fig. 6a), whereas in the W area abundances were greatest in 2007 and 2011 (Fig. 6b). The long-term average of the total zooplankton abundance was  $\sim 2$  times higher in the W area ( $\sim 10,000$  individuals  $m^{-3}$ ) compared with the CS area ( $\sim 5000$  individuals  $m^{-3}$ ) (Fig. 6). In both areas Copepod eggs and Copepod nauplii were the groups with highest abundance on average (Fig. 6), even though ZooImage might have overestimated the abundance of these two groups (Fig. 2a–b).

In the CS, approximately 40% of the *C. finmarchicus* individuals in late April consisted of recruits (i.e. copepodite stages CI–CIII) (Fig. 7a–b). The fraction of recruits varied between years, but no trend is observed. In the W area, the fraction of recruits showed different and larger fluctuations (Fig. 7c–d). During the beginning of the study period (prior to 2007) overwintered  $G_0$  individuals in the W area were dominating and young stages ( $G_1$ ) only represented  $\sim 20\%$  of the population. From 2007 and onwards the fraction of recruits fluctuated at a higher level (Fig. 7d). The years 2013 and 2016 did, however, show somewhat lower recruit fraction. The small amount of recruits present in the W area in the early study period indicates that the onset of reproduction has started shortly before the sampling. However, the reduction in abundance of  $G_0$  individuals and simultaneous increase in abundance of recruits in most years after 2007 indicates earlier onset of reproduction in the W area (Fig. 7c–d).

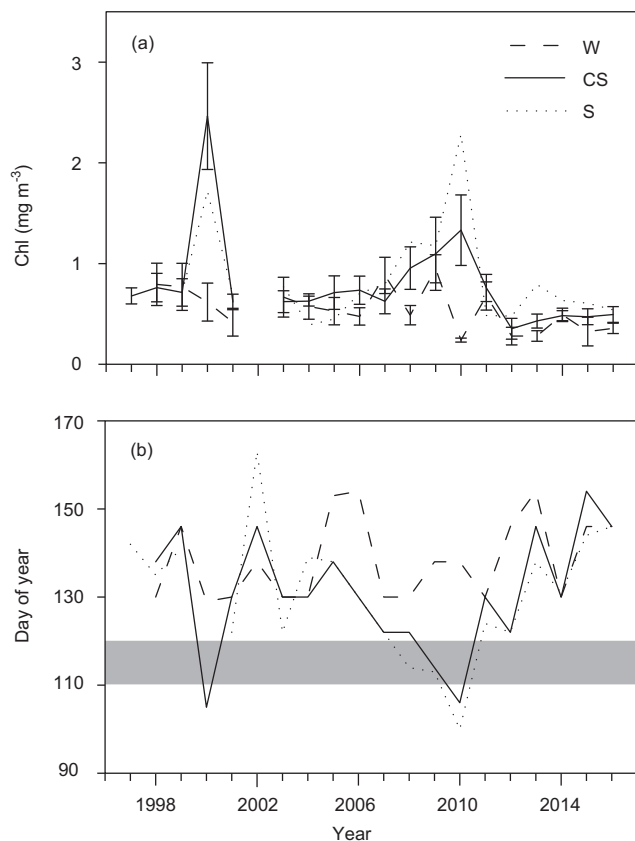


Fig. 4. (a) Average (6–50 m) chl from CTD stations in late April 1997–2016 in the CS and W area and contemporary values from coastal station S. Vertical lines show spatial standard deviation. Standard deviation was not computed for the time series from station S. (b) Associated time-series of average day number of the year derived from satellite and from station S. The shading shows the approximate time of sampling.

### 3.6. Size groups

In the CS, the smallest individuals in the zooplankton assemblage were represented by Copepod eggs, while the largest individuals were mostly constituted by *C. finmarchicus* CIV-CVI (Fig. 8a). Meroplankton and Other varied significantly in size because of the diversity of species in the zooplankton groupings (Fig. 8a). Copepod eggs, Copepod nauplii and Meroplankton dominated in the size group < 0.4 mm representing ~80% of the zooplankton in that size group (Fig. 8b). Approximately 40% of the zooplankton in the size range 0.4–1.2 mm were Meroplankton and Neritic copepods, while *C. finmarchicus* CIV-CVI represented > 50% of the zooplankton abundance in the size groups > 1.2 mm. *C. finmarchicus* CI-CIII were abundant in the size ranges 0.4–1.2 mm, but they occupied < 10% in these size groups. Zooplankton grouped as Other were represented in all size groups and were dominant in the size range 0.4–1.2 mm (Fig. 8b).

### 3.7. Environmental effects on zooplankton abundances

The potential influence of relevant environmental variables on zooplankton abundances in the CS were examined using redundancy analyses (Fig. 9). The first two axes of the RDA relating environmental variables to abundances of zooplankton species groups accounted for 88% of variability, a significant relationship ( $p = 0.045$ ) (Fig. 9a). The RDA suggests a relationship between chl within the CS and abundance of two zooplankton groups: Neritic copepods and Meroplankton, while abundance of *C. finmarchicus* CIV-CVI appears to be related to temperature. The first two axes of the RDA relating environmental variables to abundances of zooplankton grouped by size accounted for 94% of

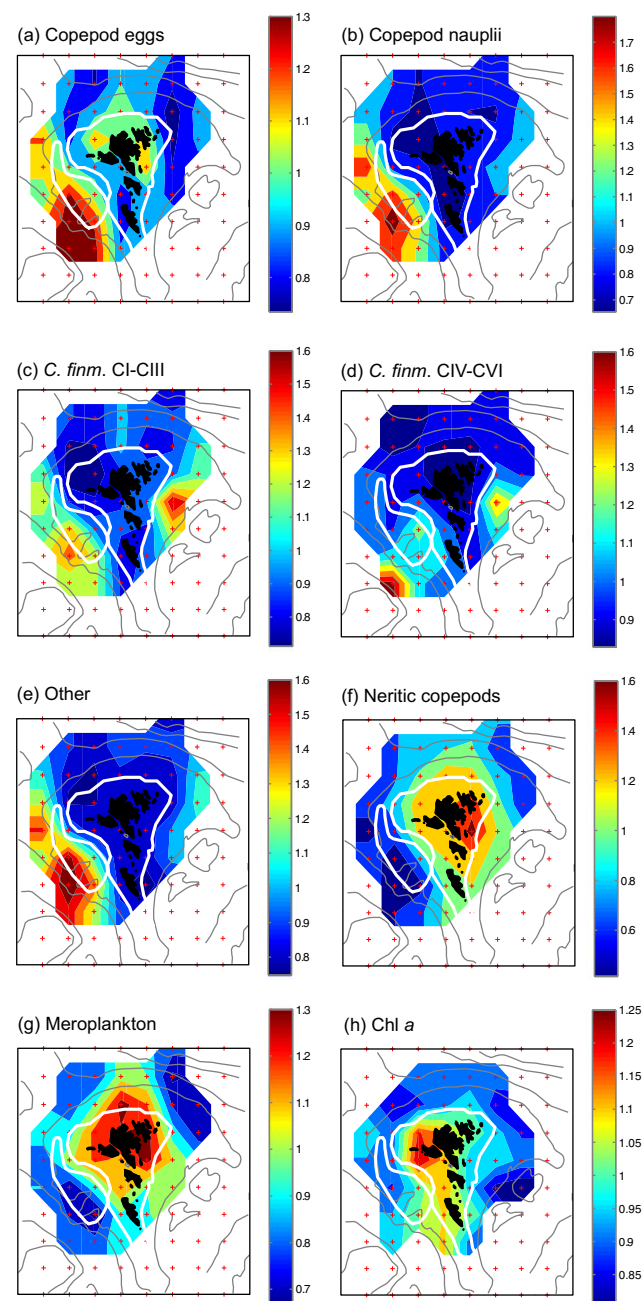


Fig. 5. Average distributions (1997–2016) of zooplankton species groups and chl over the uppermost 50 m. The data have been normalised (see Section 2.3) and are thus without units. The white lines show the average position of the front and the position of the western area, respectively. The grey lines represent 200, 500, 1000 and 1500 m bottom depth contours.

variability ( $p = 0.028$ ). Interestingly the zooplankton groups were organised in two separate clusters (ellipses on the RDA ordination for clarity of presentation) (Fig. 9b). The cluster on the positive side of the first axis contains all zooplankton < 1.2 mm, while the cluster on the negative side of the first axis contains all zooplankton  $\geq 1.2$  mm. Thus, abundance of small zooplankton is clearly associated with chl within the CS, while abundance of large zooplankton seems to be associated with temperature.

Correlation analyses (data not shown) confirmed the significant positive relationship between chl and abundance of Neritic copepods ( $r = 0.66$ ,  $p < 0.01$ ), Meroplankton ( $r = 0.92$ ,  $p < 0.0001$ ) and abundance of zooplankton in the size group 0.4–0.8 mm ( $r = 0.81$ ,  $p < 0.0001$ ). Correlation analysis also confirmed a weak positive

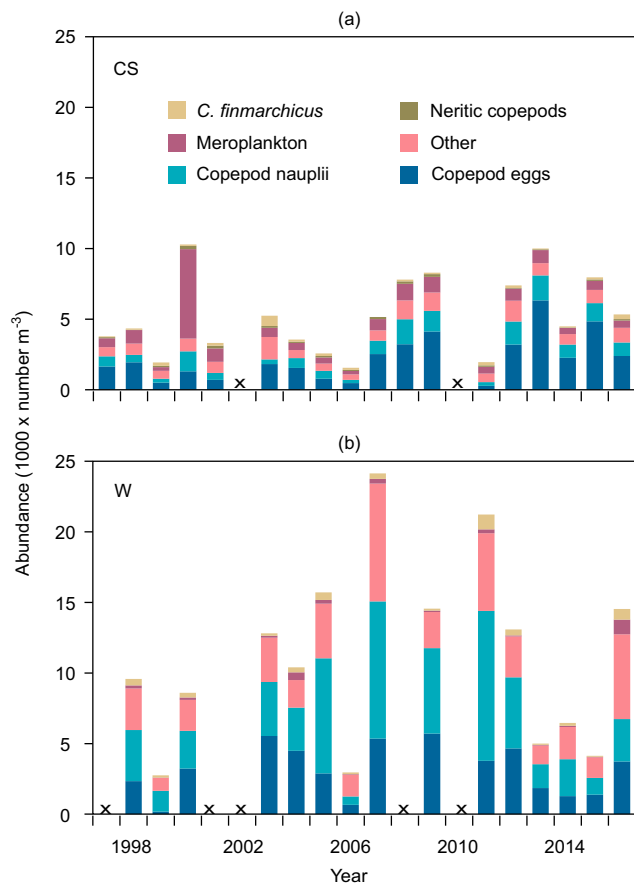


Fig. 6. Average (0–50 m) abundance of zooplankton species groups in late April 1997–2016 in the (a) CS and (b) W area. The crosses signify years with no data.

relationship between temperature and abundance of zooplankton  $> 1.6$  mm ( $r = 0.51$ ,  $p = 0.032$ ). In addition, correlation analysis indicates a weak negative relationship between chl and the exchange rate ( $k$ ) ( $r = -0.50$ ,  $p = 0.034$ ).

Similar analyses were done for the W area, but none of the selected environmental variables (i.e. temperature, salinity, chl and bloom initiation day) tested significant. The results are provided in the Supplementary Material (Fig. S7).

## 4. Discussion

### 4.1. Spatial differences in zooplankton abundances

The spatial distribution of the various plankton groups is divided in two: - some cluster around the CS and some cluster at the W area and the open ocean (Fig. 5). The spring bloom onset is on average earlier, and the chl concentration in late April is thus higher, in the CS compared with the W area (Fig. 4 and 5h). This is in agreement with previous findings (Eliassen et al., 2017; Gaard, 2000, 1996), and is most likely because phytoplankton growth in the outer waters is dependent on stratification, which usually has not set in or is only weak this early in the season (Fig. S4).

The abundance of overwintered *C. finmarchicus* (CIV-CVI) was clearly highest in the W area and in the adjacent open ocean (Figs. 5d and 7). Most likely these individuals have recently ascended from overwintering depths in the deep overflow water in the Faroe Bank Channel (Gaard and Hansen, 2000), and potentially from the Iceland Basin (Heath et al., 2000), and emerged in the upper layer in the western shelf slope region. Similarly was the average abundance of Copepod eggs and Copepod nauplii highest in the same region. These

eggs and nauplii most likely belong to *C. finmarchicus*. In spite of the fact that the fecundity of *C. finmarchicus* is largely dependent on food availability, there is also reported a significant egg production prior to the spring bloom, locally (Debes et al., 2008a; Gaard, 2000; Madsen et al., 2008) as well as in other North Atlantic regions (e.g. Jónasdóttir et al., 2008; Niehoff and Runge, 2003). Richardson et al. (1999) and Harris et al. (2000) hypothesised that internal lipid stores may partly fuel egg production of *C. finmarchicus* females, during and shortly after emerging from overwintering depths in early spring. This hypothesis is supported further by studies done in the Faroe shelf area during early spring that found relatively large amounts of wax ester lipid stores in ascendant *C. finmarchicus* (Jónasdóttir et al., 2008; Madsen et al., 2008).

In contrast to *C. finmarchicus*, Neritic copepods (*Acartia* sp. and *T. longicornis*) and also Meroplankton (larvae of benthic fauna) occurred almost exclusively in the CS, and belong to local populations. However, unlike *C. finmarchicus*, the neritic copepods do not have internal lipid stores (Kattner et al., 1981), and thus reproduction is largely dependent on concurrent food availability (Debes and Eliassen, 2006; Gaard, 1999).

By applying Objective Mapping we clearly illustrate how all the following groups: *C. finmarchicus*, Copepod eggs, Copepod nauplii and Other densely populate the oceanic waters west of the Faroe Plateau, and how these groups apparently are advected into the W area where they likely are being obstructed by the tidal front. This thus indicates that most of the oceanic species observed in the CS are advected from the W area (Fig. 5a-e), likely in localised inflow filaments (Hátún et al., 2013).

### 4.2. Plankton interannual variability

The interannual variability in zooplankton abundance is large in both areas (Fig. 6). Also, the chl concentrations and timing of spring bloom initiation in the CS are highly variable (Fig. 4). The horizontal exchange between the CS and outer shelf is suggested to affect the timing of the spring bloom in the CS (Eliassen et al., 2016, 2005; Hansen et al., 2005). This is supported by the RDAs, as the exchange rate vector points in the opposite direction of chl (Fig. 9) thereby indicating a negative relationship, which was confirmed by correlation analysis ( $r = -0.50$ ).

The correlation coefficient between chl and zooplankton abundance differs much depending on the zooplankton group considered. In the CS, the Neritic copepod abundance co-varied with the concurrent CS chl concentration ( $r = 0.66$ ), indicating a tight coupling between chl and Neritic copepod abundance with high values around year 2000 and 2008–2009 (Fig. 10). As *Acartia* sp. on average occupies 2/3 and *T. longicornis* 1/3 of the abundance in the Neritic copepod group (Table 1), this relationship might be more valid for the former species. However, overall these findings are in agreement with previous findings where abundances of the main neritic copepod species i.e. *Acartia* sp. and *T. longicornis* during spring appear to be positively linked to chl concentration (Gaard, 1999; Debes and Eliassen, 2006) even though the two species respond somewhat differently to changes in chl (Debes and Eliassen, 2006).

Also, abundance of Meroplankton was positively related with chl (Fig. 9a), indicating that survival of meroplanktonic larvae is largely influenced by the phytoplankton biomass, as well. Spawning itself is, however, most likely unaffected by phytoplankton dynamics.

Interestingly, the RDA on abundance of zooplankton grouped by sizes clearly implies that abundance of small zooplankton is largely dependent on chl (Fig. 9b). These individuals obviously include Neritic copepods and Meroplankton (Fig. 8). Connecting this finding to feeding conditions of fish larvae, which depend on small-sized food items in early spring, we therefore have reason to assume that variability in phytoplankton biomass in spring mainly seems to stimulate abundance of Neritic copepods and meroplanktonic larvae. On the other hand, abundance of *C. finmarchicus* in spring appears to be inferred by

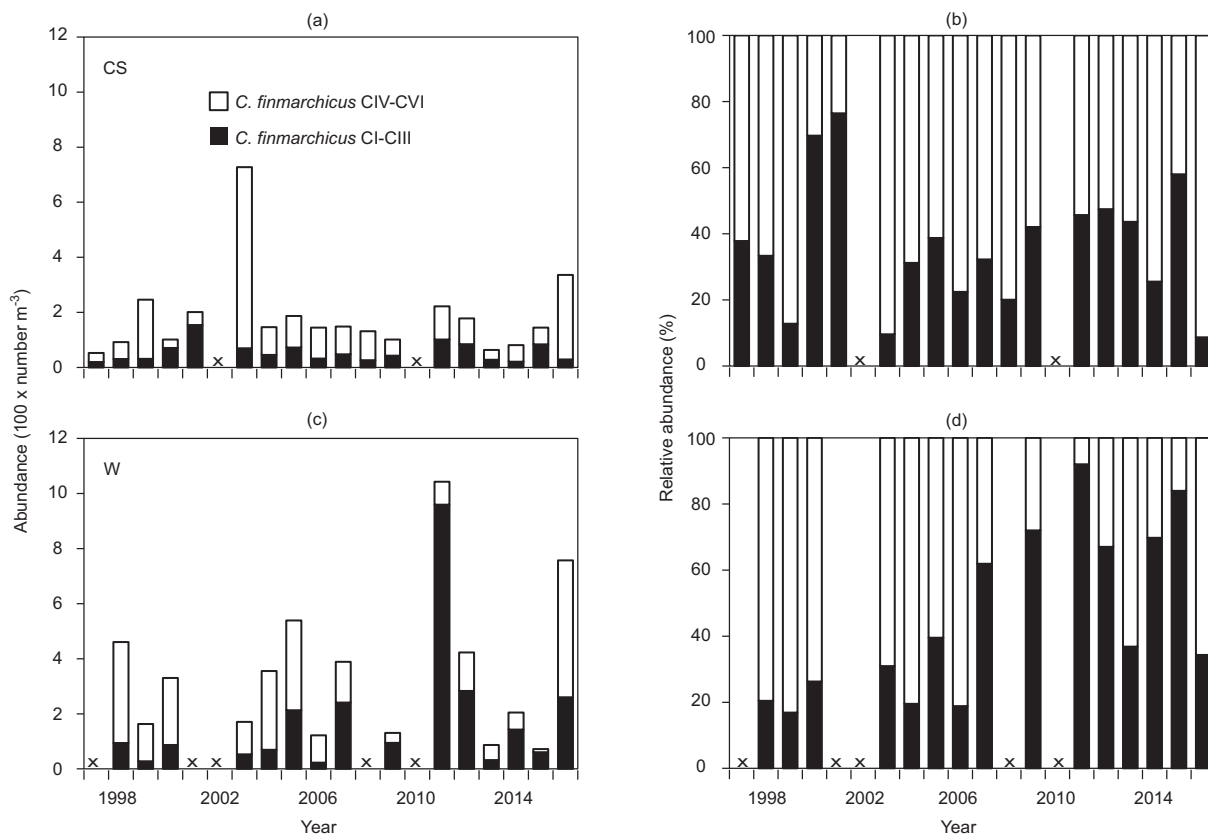


Fig. 7. *Calanus finmarchicus* abundance (left panels) and relative abundance (right panels) in late April 1997–2016 in the CS and W area (upper and lower panels respectively). The crosses signify years with no data.

advection of  $G_0$  individuals. However, once in the CS reproduction of *C. finmarchicus* is associated with the local chl concentration (Debes et al., 2008a; Gaard, 2000), and thus abundance of new generations is likely associated with a combination of advection from outer shelf waters and local reproduction of the species. This merits further research.

The Faroe shelf is devoid of *C. finmarchicus* during winter (Debes and Eliassen, 2006; Gaard, 1999), and is therefore repopulated during

spring from the overwintering populations. The interannual variability in *C. finmarchicus* abundance in early spring is therefore expected to be related to the variable oceanic abundance (Hátún et al., 2016) combined with variable advection. However, the RDA did not detect a relationship between the exchange rate ( $k$ ) and abundance of *C. finmarchicus* in the CS (Fig. 9a). Comparing with nearby regions, the total dry weight of zooplankton to the south Iceland shelf in May, which

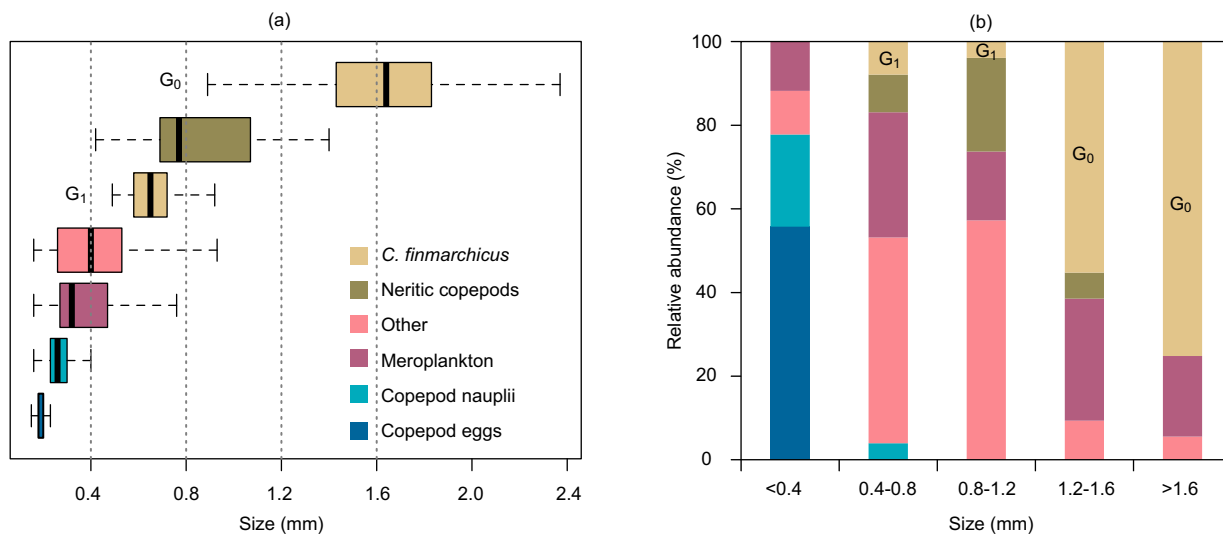
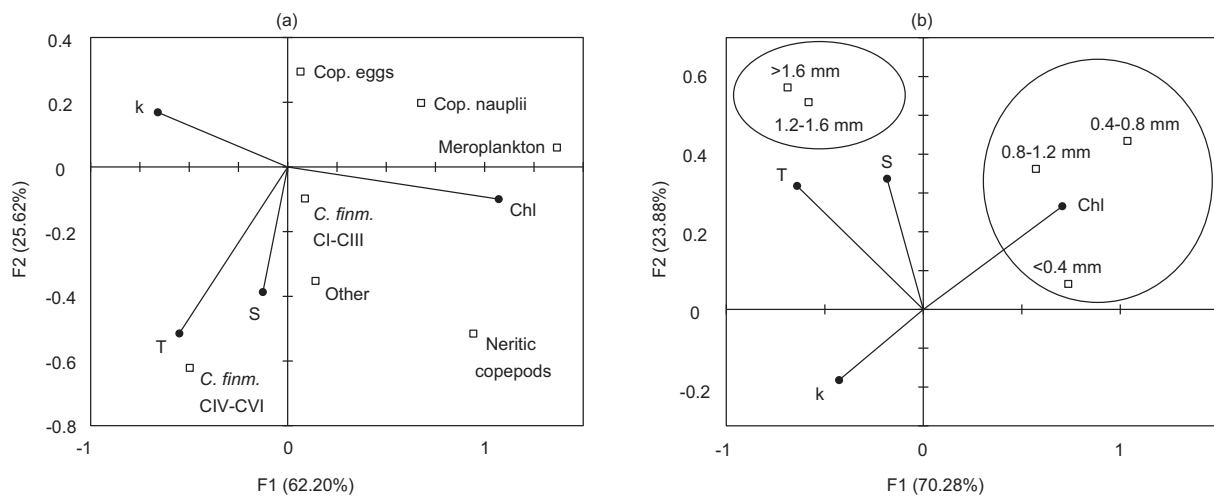
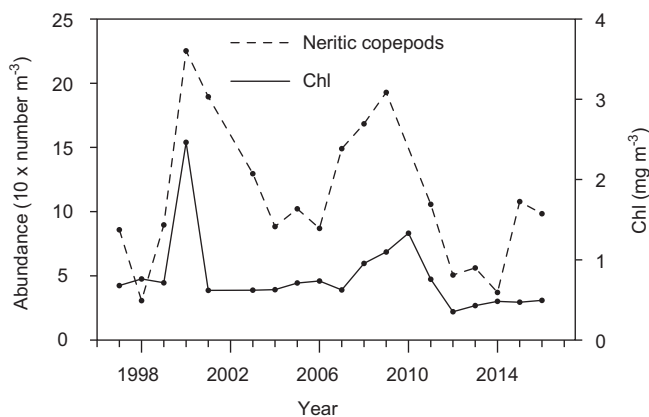


Fig. 8. (a) Box plot of zooplankton groups in the CS in late April 1997–2016 sorted by size. The line in the middle of the boxes represents the median, and the left and right ends of the box are the 25% and 75% quartiles respectively. The left and right whiskers are constructed according to R's default box plot code (R Core Team, 2014). Outliers are not shown. An equivalent box plot with outliers is provided in the Supplementary Material (Fig. S6). (b) Relative abundance of zooplankton species groups in each zooplankton size group in the CS. Note that  $G_0$  is *C. finmarchicus* CIV-CVI and  $G_1$  is *C. finmarchicus* CI-CIII.





**Fig. 9.** RDA correlation plots on abundance of (a) zooplankton species groups and (b) zooplankton size groups in the CS. Quantitative response variables (i.e. abundances of zooplankton groups) are indicated by squares and explanatory environmental variables (temperature (T), salinity (S), exchange rate (k) and chl (Chl)) are indicated by lines. The angle between two vectors is proportional to the corresponding parameters' correlation. Small angles indicate high correlations and vice versa.



**Fig. 10.** Average (0–50 m) abundance of Neritic copepods and chl concentration in the CS in late April 1997–2016.

mainly is represented by *C. finmarchicus*, exhibits strong interannual variability in synchrony with the variability within the CS ecosystem (e.g. high around 2000 and 2008–2009) (Hátún et al., 2016). Furthermore, these co-vary with the abundance of *C. finmarchicus* within the subpolar gyre (Hátún et al., 2016) and the southern Norwegian Sea gyre (Kristiansen et al., 2016; Hátún et al., 2015). Our observations of *C. finmarchicus* variability on the Faroe Plateau in late April (Fig. 7) is, however, different from the interannual *C. finmarchicus* abundance variability within the gyres. A more detailed investigation of the actual influxes of oceanic water and biological content to the Faroe Plateau is therefore warranted.

The relationships discussed above are valid for spring zooplankton abundances only. Potential niche effects such as grazing by zooplankton on phytoplankton (Debes et al., 2005; Debes et al., 2008b; Eliassen et al., 2005) or selective predation on the zooplankton (Gaard and Reinert, 2002; Gaard and Steingrund, 2001) and competition for resources in general are likely more pronounced as the season advances.

#### 4.3. *Calanus finmarchicus* phenology changes

The biological mechanisms controlling phenologic variability of zooplankton include reproductive timing of the parent generation and emergence from dormancy (Ji et al., 2010). The stage structure of *C. finmarchicus* in the outer W area changed during the study period (Fig. 7d) indicating variable times of moulting and spawning of this

copepod. The spawning seems to have started earlier since around 2007, however in 2013 and 2016 it seems again to have started somewhat late. Changes in phenology seem to be strongly related to water masses and temperature (Ji et al., 2010; Mackas and Beaugrand, 2010). Clark et al. (2012) suggested that duration of dormancy is determined by the rate of storage lipid utilisation, which is temperature dependent and regulated by storage lipid composition (Pierson et al., 2013). There was a sharp increase in temperature both in the CS and W area in 2003 (Fig. 3a). However, the phenological shift in *C. finmarchicus* reproduction in the W area occurred four years later than the shift in temperature (Fig. 3a), and multivariate statistics could not detect a relationship between temperature or any of the other selected environmental variables (i.e. chl, bloom initiation day and/or salinity) and the observed changes in *C. finmarchicus* stage abundance (Fig. S7). In addition, according to the temperature-dependent development rates given by Miller and Tande (1993) and Campbell et al. (2001), a temperature increase of 1 °C would only shorten the development time from egg to CIII by ~4 days, which is not sufficient to explain the phenological change observed in the Faroe shelf area. Thus, the phenological shift can probably not be caused by faster developmental rates due to temperature increase alone. According to Hansen et al. (2016) the temperature in the cold deep overflow water in the Faroe Bank Channel has increased by 0.1 °C and the majority of this increase occurred in 2004–2005, which is only 1–2 years before the increased proportion of G<sub>1</sub> copepodites (CI–CIII) in late April. This water contains overwintered *C. finmarchicus* and it may therefore be questioned whether the increase in overwintering temperature of *C. finmarchicus* may have shortened the time length of diapause or earlier moulting and gonad maturation. Recently, a similar phenological shift of *C. finmarchicus* has been reported north of the Faroe Islands in the southwestern Norwegian Sea (Kristiansen et al., 2016), and this shift was proposed to be caused by a westward retraction of cold and low-saline East Icelandic Water.

Changes in food supply may also alter the reproductive activity of zooplankton. At the temperatures that are common in the Atlantic waters in April (~8 °C) the *C. finmarchicus* CI–CIII copepodites, which occurred in the Faroe shelf area, were spawned 3–5 weeks prior to sampling (Campbell et al., 2001; Miller and Tande, 1993), i.e. second half of March. At this time of year the chl concentrations usually are below 0.3–0.4 mg m<sup>-3</sup> and phytoplankton may therefore not be the primary contributor to production of these individuals. However, Backhaus et al. (1999) found that west of the Faroe Plateau, deep winter convection sustains an overwintering diatom spore population, which provides an inoculum for a spring bloom, and very small

increases in phytoplankton biomass were found already during the pre-bloom period (i.e. in March). Strong inter-annual variability in winter convection depth could therefore impact the *C. finmarchicus* phenology (Hátún et al., 2016) through variable deep food production and/or through an interaction between the variable vertical convective motion and the re-surfacing of these copepods (Backhaus et al., 2003).

With regard to the Faroe shelf area, it is conspicuous that the phenology shift was not observed in the CS (Fig. 7). Three main reasons for the discrepancy are suggested: 1) slower development of the population in the colder CS water, 2) the variable advection and 3) the shift is masked by the relatively high phytoplankton variability in the CS. Yet, it is likely that the shift in the W area affects the abundance and stage composition of *C. finmarchicus* in the CS in spring as well.

Interestingly, the Atlantic mackerel (*Scomber scombrus*) stock, which mainly preys on *C. finmarchicus* (Prokopchuk and Sentyabov, 2006), expanded and increased markedly in and north of the Faroe area around the same time of the *C. finmarchicus* phenological change (Nøttestad et al., 2016).

## 5. Conclusions

We here show that variability in the abundance of Neritic copepods and Meroplankton, and in all zooplankton types smaller than 1.2 mm within the central Faroe shelf in spring, is considerably dependent on the local chlorophyll concentration. The interannual variability of these plankton types shows increased abundance around 2000 and 2008–2009. The abundance of overwintered *Calanus finmarchicus*, Copepod eggs, Copepod nauplii and other is highest to the west of the shelf, and these groups are therefore likely transported to the central shelf area from the western oceanic waters. The abundance of these groups in the central shelf area must thus depend on both the ocean-shelf exchange rate and on the oceanic plankton concentrations. We reveal changes in *C. finmarchicus* phenology in the outer western shelf area, resulting in earlier onset of reproduction in late winter/early spring after 2006 with few exceptions (i.e. in 2013 and 2016). The variability in *C. finmarchicus* abundance cannot be explained by the herein tested environmental explanatory variables, and the stock does not reflect the characteristic ecosystem variability observed on the Faroe shelf. Whether the *C. finmarchicus* change is related to an observed temperature increase in overwintering water masses, convective activity, changes in food supply or other processes needs to be investigated further.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2017.08.004>.

## References

- Backhiller, E., Fernandes, J.A., 2011. Zooplankton Image Analysis Manual: automated identification by means of scanner and digital camera as imaging devices. *Rev. Invest. Mar.* 18, 16–37.
- Backhaus, J.O., Wehde, H., Hegseth, E.N., Kämpf, J., 1999. “Phyto-convection”: the role of oceanic convection in primary production. *Mar. Ecol. Prog. Ser.* 189, 77–92. <http://dx.doi.org/10.3354/meps189077>.
- Backhaus, J.O., Hegseth, E.N., Wehde, H., Irigoien, X., Hatten, K., Logemann, K., 2003. Convection and primary production in winter. *Mar. Ecol. Prog. Ser.* 251, 1–14. <http://dx.doi.org/10.3354/meps251001>.
- Bell, J.L., Hopcroft, R.R., 2008. Assessment of ZoolImage as a tool for the classification of zooplankton. *J. Plankton Res.* 30, 1351–1367. <http://dx.doi.org/10.1093/plankt/fbn092>.
- Böhme, L., Send, U., 2005. Objective analyses of hydrographic data for referencing profiling float salinities in highly variable environments. *Deep-Sea Res. II Top. Stud. Oceanogr.* 52, 651–664. <http://dx.doi.org/10.1016/j.jdsr.2004.12.014>.
- Breiman, L., 2001. Random Forests. *Mach. Learn.* 45, 5–32. <http://dx.doi.org/10.1023/A:1010933404324>.
- Campbell, R., Wagner, M., Teegarden, G., Boudreau, C., Durbin, E., 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol. Prog. Ser.* 221, 161–183. <http://dx.doi.org/10.3354/meps221161>.
- Clark, K.A.J., Brierley, A.S., Pond, D.W., 2012. Composition of wax esters is linked to diapause behavior of *Calanus finmarchicus* in a sea loch environment. *Limnol. Oceanogr.* 57, 65–75. <http://dx.doi.org/10.4319/lo.2012.57.1.0065>.
- Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL <http://www.R-project.org/>).
- Culverhouse, P.F., Ellis, R., Simpson, R.G., Williams, R., Pierce, R.W., Turner, J.T., 1994. Automatic categorisation of five species of *Cymatocylis* (Protozoa, Tintinnida) by artificial neural network. *Mar. Ecol. Prog. Ser.* 107, 273–280. <http://dx.doi.org/10.2307/24842683>.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the Match/Mismatch hypothesis. *Adv. Mar. Biol.* 26, 249–293.
- Debes, H.H., Eliassen, K., 2006. Seasonal abundance, reproduction and development of four key copepod species on the Faroe shelf. *Mar. Biol. Res.* 2, 249–259.
- Debes, H.H., Hansen, B.W., Hansen, P.J., 2005. The relative importance of protozooplankton and copepods as grazers on phytoplankton during a spring bloom situation on the Faroe Shelf. *Frøðskaparrít 53*, 82–99.
- Debes, H., Eliassen, K., Gaard, E., 2008a. Seasonal variability in copepod ingestion and egg production on the Faroe shelf. *Hydrobiologia* 600, 247–265. <http://dx.doi.org/10.1007/s10750-007-9238-3>.
- Debes, H., Gaard, E., Hansen, B., 2008b. Primary production on the Faroe shelf: Temporal variability and environmental influences. *J. Mar. Syst.* 74, 686–697. <http://dx.doi.org/10.1016/j.jmarsys.2008.07.004>.
- Di Mauro, R., Cepeda, G., Capitanio, F., Viñas, M.D., 2011. Using ZoolImage automated system for the estimation of biovolume of copepods from the northern Argentine Sea. *J. Sea Res.* 66, 69–75. <http://dx.doi.org/10.1016/j.seares.2011.04.013>.
- Eliassen, S.K., Gaard, E., Hansen, B., Larsen, K.M.H., 2005. A “horizontal Sverdrup mechanism” may control the spring bloom around small oceanic islands and over banks. *J. Mar. Syst.* 56, 352–362. <http://dx.doi.org/10.1016/j.jmarsys.2005.03.005>.
- Eliassen, K., Reinert, J., Gaard, E., Hansen, B., Jacobsen, J.A., Christensen, J.T., Grønkjær, P., 2011. Saaedee as a link between primary production and higher trophic levels on the Faroe shelf. *Mar. Ecol. Prog. Ser.* (doi:10.3354/meps09301).
- Eliassen, S.K., Hansen, B., Larsen, K.M.H., Hátún, H., 2016. The exchange of water between the Faroe Shelf and the surrounding waters and its effect on the primary production. *J. Mar. Syst.* 153, 1–9. <http://dx.doi.org/10.1016/j.jmarsys.2015.08.004>.
- Eliassen, S.K., Hátún, H., Larsen, K.M.H., Hansen, B., Rasmussen, T.A.S., 2017. Phenologically distinct phytoplankton regions on the Faroe Shelf - identified by satellite data, *in-situ* observations and model. *J. Mar. Syst.* 169, 99–110. <http://dx.doi.org/10.1016/j.jmarsys.2017.01.015>.
- Embleton, K.V., Gibson, C.E., Heaney, S.I., 2003. Automated counting of phytoplankton by pattern recognition: a comparison with a manual counting method. *J. Plankton Res.* 25, 669–681. <http://dx.doi.org/10.1093/plankt/25.6.669>.
- Frank, K.T., Leggett, W.C., 1986. Effect of prey abundance and size on the growth and survival of larval fish: an experimental study employing large volume enclosures. *Mar. Ecol. Prog. Ser.* 34, 11–22.
- Gaard, E., 1996. Phytoplankton community structure on the Faroe Shelf. *Frøðskaparrít 44*, 95–106.
- Gaard, E., 1999. The zooplankton community structure in relation to its biological and physical environment on the Faroe shelf, 1989–1997. *J. Plankton Res.* 21, 1133–1152.
- Gaard, E., 2000. Seasonal abundance and development of *Calanus finmarchicus* in relation to phytoplankton and hydrography on the Faroe Shelf. *ICES J. Mar. Sci.* 57, 1605–1611. <http://dx.doi.org/10.1006/jmsc.2000.0963>.
- Gaard, E., 2003. Plankton variability on the Faroe Shelf during the 1990s. *ICES Mar. Sci. Symp.* 219, 182–189.
- Gaard, E., Hansen, B., 2000. Variations in the advection of *Calanus finmarchicus* onto the Faroe Shelf. *ICES J. Mar. Sci.* 57, 1612–1618. <http://dx.doi.org/10.1006/jmsc.2000.0962>.
- Gaard, E., Reinert, J., 2002. Pelagic cod and haddock juveniles on the Faroe plateau: distribution, diets and feeding habits, 1994–1996. *Sarsia* 87, 193–206. <http://dx.doi.org/10.1080/00364820260294833>.
- Gaard, E., Steingrund, P., 2001. Reproduction of faroe plateau cod: spawning grounds, egg advection and larval feeding. *Frøðskaparrít 48*, 87–103.
- Gaard, E., Hansen, B., Olsen, B., Reinert, J., 2002. 8 Ecological features and recent trends in the physical environment, plankton, fish stocks, and seabirds in the Faroe shelf ecosystem. *Large Marine Ecosystems* 10, 245–265. [http://dx.doi.org/10.1016/S1570-0461\(02\)80060-X](http://dx.doi.org/10.1016/S1570-0461(02)80060-X).
- Gislason, A., Silva, T., 2009. Comparison between automated analysis of zooplankton using ZoolImage and traditional methodology. *J. Plankton Res.* 31, 1505–1516. <http://dx.doi.org/10.1093/plankt/fbp094>.
- Grosjean, P., Denis, K., 2007. Zoo/PhytoImage Version 1.2-0 Computer-Assisted Plankton Image Analysis User's Manual.
- Hansen, B., Østerhus, S., 2000. North Atlantic–Nordic Seas exchanges. *Prog. Oceanogr.* 45, 109–208. [http://dx.doi.org/10.1016/S0079-6611\(99\)00052-X](http://dx.doi.org/10.1016/S0079-6611(99)00052-X).
- Hansen, B., Eliassen, S.K., Gaard, E., Larsen, K.M.H., 2005. Climatic effects on plankton and productivity on the Faroe Shelf. *ICES J. Mar. Sci.* 62, 1224–1232. <http://dx.doi.org/10.1016/j.jicesjms.2005.04.014>.
- Hansen, B., Larsen, K.M.H., Hátún, H., Østerhus, S., 2016. A stable Faroe Bank Channel overflow 1995–2015. *Ocean Sci.* 12, 1205–1220. <http://dx.doi.org/10.5194/os-12->

- 1205-2016.
- Harris, R., Irigoien, X., Head, R.N., Rey, C., Hygum, B.H., Hansen, B.W., Niehoff, B., Meyer-Harms, B., Carlotti, F., 2000. Feeding, growth, and reproduction in the genus *Calanus*. ICES J. Mar. Sci. 57, 1708–1726. <http://dx.doi.org/10.1006/jmsc.2000.0959>.
- Hátún, H., Larsen, K., Debes, H., 2013. The Western region. In: Technical report Nr.: 13-07. Havstovan, Faroe Islands. <http://www.hav.fo/PDF/Ritgerdir/2013/TecRep1307.pdf>.
- Hátún, H., Pacariz, S., Jacobsen, J.A., Sentyabov, E., Kalashnikov, Y., Krysov, A., 2015. Marine climate and mackerel distribution. In: Annex to the 39. Joint Faroese - Russian Fisheries Commission, Nov. 2015.
- Hátún, H., Lohmann, K., Matei, D., Jungclaus, J.H., Pacariz, S., Bersch, M., Gislason, A., Ólafsson, J., Reid, P.C., 2016. An inflated subpolar gyre blows life toward the northeastern Atlantic. Prog. Oceanogr. 147, 49–66. <http://dx.doi.org/10.1016/j.pocean.2016.07.009>.
- Heath, M.R., Jónasdóttir, S.H., 1999. Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe-Shetland Channel. Fish. Oceanogr. 8, 40–60. <http://dx.doi.org/10.1046/j.1365-2419.1999.00012.x>.
- Heath, M., Fraser, J.G., Gislason, A., Hay, S.J., Jónasdóttir, S.H., Richardson, K., 2000. Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic. ICES J. Mar. Sci. 57, 1628–1635. <http://dx.doi.org/10.1006/jmsc.2000.0978>.
- Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. In: Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer 20, 228. (doi:c:\Pubs\Classics). ICES, 2016. Report of the North-Western Working Group (NWWG) 2016. (ICES C.M. 2016/ACOM:08, 2016).
- Irigoien, X., Fernandes, J.A., Grosjean, P., Denis, K., Albaina, A., Santos, M., 2008. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. J. Plankton Res. 31, 1–17. <http://dx.doi.org/10.1093/plankt/fbn096>.
- Ji, R., Edwards, M., Mackas, D.L., Runge, J.A., Thomas, A.C., 2010. Marine plankton phenology and life history in a changing climate: current research and future directions. J. Plankton Res. 32, 1355–1368. <http://dx.doi.org/10.1093/plankt/fbq062>.
- Jónasdóttir, S.H., Richardson, K., Heath, M.R., Ingvarsdóttir, A., Christoffersen, A., 2008. Spring production of *Calanus finmarchicus* at the Iceland–Scotland Ridge. Deep-Sea Res. I Oceanogr. Res. Pap. 55, 471–489. <http://dx.doi.org/10.1016/j.dsr.2007.12.009>.
- Kattner, G., Krause, M., Trahms, J., 1981. Lipid Composition of Some Typical North Sea Copepods. Vol. 4. pp. 69–74.
- Kristiansen, I., Gaard, E., Hátún, H., Jónasdóttir, S., Ferreira, A.S.A., 2016. Persistent shift of *Calanus* spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. ICES J. Mar. Sci. 1319–1329. <http://dx.doi.org/10.1093/icesjms/fsv222>.
- Lance, G.N., Williams, W.T., 1967. A general theory of classificatory sorting strategies: II. Clustering systems. Comput. J. 10, 271–277. <http://dx.doi.org/10.1093/comjnl/10.3.271>.
- Larsen, K.M.H., Hansen, B., Svendsen, H., 2008. Faroe Shelf Water. Cont. Shelf Res. 28, 1754–1768. <http://dx.doi.org/10.1016/j.csr.2008.04.006>.
- Larsen, K.M.H., Hansen, B., Svendsen, H., 2009. The Faroe Shelf Front: Properties and exchange. J. Mar. Syst. 78, 9–17. <http://dx.doi.org/10.1016/j.jmarsys.2009.02.003>.
- Larsen, K.M.H., Hátún, H., Hansen, B., Kristiansen, R., 2012. Atlantic water in the Faroe area: sources and variability. ICES J. Mar. Sci. 69, 802–808. <http://dx.doi.org/10.1093/icesjms/fss028>.
- Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier Science, Amsterdam (p. 839).
- Lindgren, J.F., Hassellöv, I.-M., Dahllöf, I., 2013. Analyzing changes in sediment meiofauna communities using the image analysis software ZoolImage. J. Exp. Mar. Biol. Ecol. 440, 74–80. <http://dx.doi.org/10.1016/j.jembe.2012.12.001>.
- Mackas, D.L., Beaugrand, G., 2010. Comparisons of zooplankton time series. J. Mar. Syst. 79, 286–304. <http://dx.doi.org/10.1016/j.jmarsys.2008.11.030>.
- Madsen, M.L., Gaard, E., Hansen, B.W., 2008. Wax-ester mobilization by female *Calanus finmarchicus* (Gunnerus) during spring ascendance and advection to the Faroe Shelf. ICES J. Mar. Sci. 65, 1112–1121. <http://dx.doi.org/10.1093/icesjms/fsn097>.
- Maritorena, S., Siegel, D.A., Peterson, A.R., 2002. Optimization of a semi-analytical ocean color model for global-scale applications. Appl. Opt. 41, 2705. <http://dx.doi.org/10.1364/AO.41.002705>.
- Miller, C.B., Tande, K.S., 1993. Stage duration estimation for *Calanus* populations, a modelling study. Mar. Ecol. Prog. Ser. 102, 15–34.
- Niehoff, B., Runge, J.A., 2003. A revised methodology for prediction of egg production *Calanus finmarchicus* from preserved samples. J. Plankton Res. 25, 1581–1587. <http://dx.doi.org/10.1093/plankt/fbg104>.
- Nøttestad, L., Utne, K.R., Óskarsson, G.J., Jónsson, S.P., Jacobsen, J.A., Tangen, Ø., Anthonypillai, V., Aanes, S., Vølstad, J.H., Bernasconi, M., Debes, H., Smith, L., Sveinbjörnsson, S., Holst, J.C., Jansen, T., Slotte, A., 2016. Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. ICES J. Mar. Sci. 73, 359–373. <http://dx.doi.org/10.1093/icesjms/fsv218>.
- Parsons, T.R., Maita, Y., Lalli, C.M., 1984. Related Pergamon titles of interest. In: A Manual of Chemical & Biological Methods for Seawater Analysis. Pergamon Press p. 173. <https://doi.org/10.1016/B978-0-08-030287-4.50001-3>.
- Pierson, J.J., Batchelder, H., Saumweber, W., Leising, A., Runge, J., 2013. The impact of increasing temperatures on dormancy duration in *Calanus finmarchicus*. J. Plankton Res. 35, 504–512. <http://dx.doi.org/10.1093/plankt/fbt022>.
- Prokopchuk, I., Sentyabov, E., 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES J. Mar. Sci. 63, 117–127. <http://dx.doi.org/10.1016/j.icesjms.2005.08.005>.
- Rasmussen, T.A.S., Olsen, S.M., Hansen, B., Hátún, H., Larsen, K.M.H., 2014. The Faroe shelf circulation and its potential impact on the primary production. Cont. Shelf Res. 88, 171–184. <http://dx.doi.org/10.1016/j.csr.2014.07.014>.
- Richardson, K., Jónasdóttir, S.H., Hay, S.J., Christoffersen, A., 1999. *Calanus finmarchicus* egg production and food availability in the Faroe-Shetland Channel and northern North Sea: October–March. Fish. Oceanogr. 8, 153–162. <http://dx.doi.org/10.1046/j.1365-2419.1999.00007.x>.
- Steingrund, P., Gaard, E., 2005. Relationship between phytoplankton production and cod production on the Faroe Shelf. ICES J. Mar. Sci. 62, 163–176. <http://dx.doi.org/10.1016/j.icesjms.2004.08.019>.
- Steingrund, P., Hansen, B., Gaard, E., 2005. Cod in Faroese Waters. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report 274, 50–55.
- Vu, M.T.T., Jepsen, P.M., Hansen, B.W., 2014. A comprehensive and precise quantification of the calanoid copepod *Acartia tonsa* (Dana) for intensive live feed cultures using an automated ZoolImage system. Aquaculture 422–423, 225–231. <http://dx.doi.org/10.1016/j.aquaculture.2013.12.002>.